Mr. Tegetemier exhibited and made remarks on some heads of the Sumatran Rhinoceros (*Rh. sumatrensis*), male, female, and young, forwarded from Sarawak, Borneo, by Mr. Brooke-Lowe.

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Prof. Bell exhibited a specimen of *Nereis pelagica* which he had received from his excellent correspondent Mr. R. L. Spencer of Guernsey, and which was remarkable for the bifid arrangement of the posterior portion of the body. He remarked that although Mr. Robertson, of Oxford, Dr. Horst, and himself had put on record Lumbrici with trifid ends, which probably were not really uncommon, he had not been able to find any record of a similar condition in a Polychæte.

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A communication was read from Messrs. H. B. Brady, F.R.S., W. K. Parker, F.R.S., and T. Rupert Jones, F.R.S., containing an account of the Foraminifera procured on the Abrohlos Bank during the cruise of H.M.S. 'Plumper' in 1857.

This memoir will be printed in the Society's 'Transactions.'

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The following papers were read :—

## 1. On the Skeleton and Affinities of the Paired Fins of *Ceratodus*, with Observations upon those of the *Elasmobranchii*. By G. B. Howes, F.Z.S., F.L.S., Assist. Prof. of Zoology, Normal School of Science and Royal School of Mines, S. Kensington.

[Received December 14, 1886.]

(Plates I.–III.)

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### I. *Introduction.*

I have lately described (17, p. 277) the vertebral column of a Frog in connexion with which there had taken place, under dislocation of the urostyle, a process tantamount to that of reproduction of a lost part. While searching for literature bearing upon this subject,

there came under my notice a short paper by Traquair (26, p. 143), in which he describes the restoration of parts of the tail of *Protopterus*. Finding that he had discovered certain irregularities in the skeletal elements of the said restored tails, and knowing that Haswell had recorded (15) some irregularities of the *Ceratodus* paired fins, it occurred to me that the same determining cause might have been at work in the two cases—*i. e.*, that Haswell's "branching" fins might perchance be "restored" ones, like Traquair's. I was soon undeceived; for, apart from Haswell's paper, I have had the good fortune to examine one such fin, sent by him to Prof. Huxley. The deductions arrived at in the sequel have arisen out of a study of it and of the fins of five other individuals. Three of them were kindly lent me by my master, Prof. Huxley; of the two which remain, one forms part of our teaching-collection at South Kensington; for the loan of the other I am indebted to my Demonstrator, Mr. M. F. Woodward.

It is remarkable that Günther, in his Monograph on *Ceratodus* (14), does not mention Traquair's discovery already alluded to. It is clear that that author's paper must have escaped him, as I fail to find note of it under either "*Pisces*" or "*Ganoidei*," as reported by him for the 'Zoological Record' during both its year of publication and the succeeding one.

The structural plan of the fin of *Ceratodus* is too familiar to merit detailed description here. Huxley has described (19, p. 46 *et seq.*) its general features with exceeding care, and I shall, in accordance with his system, speak of the segments of the axis as "*mesomeres*."

The lateral rays will be described, under the same nomenclature, as *parameres*; those which look dorsally when the fin is placed against the side wall of the body (anteriorly when it is held out at right angles thereto) I shall speak of as *preaxial*; those which look ventrally under the first-named condition (posteriorly under the last-named) I shall describe as *postaxial*. Preaxial and postaxial correspond to the "dorsal" and "ventral" of the Germans. As the basal segment of the axis differs in its essential characters from those which follow upon it, I shall refer to it as the *proximal mesomere* (the "zwischen-Stuck" of Davidoff (7), the "erste Glied" of Schneider (23)).

## II. *On the Structure of the* Ceratodus *Paired Fins in general and of the Pelvic Fins in particular.*

The majority of observations made thus far upon the fins of *Ceratodus* bear especially upon the pectoral member; its pelvic representative has received less attention. Davidoff (7) and Haswell (15) have dealt most fully with it, the last-named author especially as to certain "irregularities" mentioned in the Introduction. Fig. 1 is a faithful representation of the pelvic fin presented by him to Prof. Huxley; and as it does not appear to correspond with any one figured in his own paper, I proceed to describe it in detail.

The fin reached me cleaned and prepared, as represented in the

figure, and it had first to be ascertained from which side of the body it was derived. Its proximal mesomere (*m.p.*, fig. 1) carries a large tubercle (*tb.*), which, as Schneider has lately pointed out, "bei der Brustflosse ventral, bei der Bauchflosse dorsal steht"—when the limb is in apposition with the body-wall. This process is, in all pelvic fins examined by me, somewhat crescent-shaped and outwardly directed, its inner face being excavated. In the fin under discussion its outer surface was flattened; but as its inner one sloped obliquely outwards, I conclude that that fin was a right-sided one. It is represented in the figure as seen from the dorsal aspect. Its axis is for the most part unequally segmented and irregular, the proximal mesomere being the least modified portion thereof, as compared with the more normal fin. The second mesomere is greatly elongated, and it bears upon its postaxial border (left hand of the figure) a notched lobe, with which are connected five parameres. The two distal of these break up peripherally, and, on examining the individual specimen, it is hard to conjecture how far the lines of demarcation between the parameres and the lobe, and between it and the main piece of the axis, may represent the last traces of original lines of separation, or the lines of cleavage of a primarily continuous sheet. Preaxially, the second mesomere carries five parameres; these are fairly uniformly set upon it, and the distal one of the series branches in a true dichotomy. Interposed between the free ends of the two proximal of these rays there is a smaller one (marked * in the figure), which I take to resemble those found by Davidoff (7, p. 127), occasionally lying free at the distal end of the fin. The rest of the skeleton is chiefly remarkable as concerns the axis; this appears to be longitudinally cleft, and made up of a longer preaxial and a shorter postaxial piece, both of which are very irregularly segmented. All the parameres borne upon it, however, are simple unbranched rods, which differ from those more generally present only as regards their feeble segmentation.

On examining the above-named fin with care, my attention became arrested by the cartilage marked *r* in the figure, the characters and relations of which are altogether exceptional. Wiedersheim has called attention (30) to the fact that in *Protopterus* the basal segment of the axis may bear a lateral piece. To the consideration of this I shall return. In no regular *Ceratodus* fin (*i. e.* that bearing an equally segmented axis) yet described has there been found, postaxially, a cartilage like the above named, attached directly to the basal mesomere. That element is generally held to be destitute of rays. Günther has figured (14, pl. 36. fig. 4) a pelvic fin of the right side, which bears lateral cartilages in the above-named region; but I find no mention of the fact in his text. It is to me inexplicable for what reason he should have failed to describe so remarkable a feature. I shall return, in the sequel, to the discussion of this fin. Haswell has figured and described (15, figs. 5, 6, 7 [1])

[1] His fig. 2 is said to be a representation in outline of the pectoral fin, after Huxley. It is unfortunate that the bounday-line between the two basal mesomeres, indicated in the original, should have been omitted.

what I imagine may represent the cartilage in question, and that, as is here the case, in irregular fins. Be it, as it there exists, what it may, its characters in the fin figured by me are still further noteworthy. The entire fin-skeleton (fig. 1), with the exception of this bar and the proximal mesomere, is very slender and leaf-like; the two elements just named (which, be it remembered, are in direct connexion) are relatively massive and much thicker and more powerful than the rest. The bar *r*, instead of being ellipsoidal in transverse section, as is invariably the case with even the most powerful parameres, is expanded along its free border in a manner strikingly suggestive of the metapterygium as it exists in many Elasmobranchs. It is segmented into a main piece and two small terminal ones, and appears, at first sight, to represent an element of greater importance than an ordinary ray.

The fact that this new element appears in "irregular" fins, taken in conjunction with the fact that no such structure has hitherto been recorded for a "regular" fin, appears at first sight to detract from its novelty. Before proceeding further, therefore, three questions must be met:—1. How far is the fin under discussion abnormal? 2. Can the existence of the new element be demonstrated for a more normal fin?, and 3. If so, under what structural conditions does it exist? Günther, in his original description of the *Ceratodus* fin, described (14, p. 532) certain "slight irregularities" in the distribution of the rays. Huxley (19, p. 47), commenting upon these, remarks that they are "in respect of the median pieces . . . . constant peculiarities of no small importance." Davidoff (7, p. 126) describes the stem of the pelvic fin as consisting of a row of pieces "deren Zahl bei den verschiedenen Individuen beträchtlich variirt;" he adds—"nirgends fand ich ein so unregelmässiges Verhältniss derselben zu einander, wie es Günther auf seiner Figur abbildet." Other writers have observed this irregularity, and the last of them (Schneider) has formulated the distribution of the parameres of both fins. He states (23, pp. 521–22), "bei der Brustflosse sitzt dorsalwärts am zweiten bis elften Gliede des Hauptstrahls, und zwar an der distalen Gelenkfläche, je ein Seitenstrahl. Ventralwarts sitzen am zweiten Gliede des Hauptstrahls hinter einander fünf Seitenstrahlen, am dritten und vierten Gliede je zwei, an den folgenden einer. Bei der Bauchflosse tragen die Glieder des Hauptstrahls ventralwärts je einen Seitenstrahl, dorsalwärts je zwei Seitenstrahlen." I have taken some pains to test the reliability of this very definite statement, and am in a position to assert with equal assurance that *the* only constant character as yet recognized is the attachment of one ray to the preaxial border of each pectoral mesomere (*cf.* figs. 5 & 6). Even in so modified a fin as that of fig. 5, where several of the parameres are branched and two are directly confluent, this rule holds; and in no regular pectoral fin yet examined has an exception to it been found. I give below a table of average distribution of the parameres of those segments dealt with by Schneider, calculated out from observations made upon eight pectoral and ten pelvic fins.

*Pectoral fin.*

| | Postaxial. | | | | Preaxial. |
|---|---|---|---|---|---|
| | Seg. ii. | iii. | iv. | v. | ii. |
| Schneider .... | 5 | 2 | 2 | 1 | 1 |
| Observed .... | 3·5 | 1·9 | 1·6 | 1·3 | 1 |

*Pelvic fin.*

| | Postaxial. | Preaxial. |
|---|---|---|
| | Seg. ii. | ii. |
| Schneider.... | 1 | 2 |
| Observed .... | 2·1 | 2·5 |

Further comment upon the pectoral member may be deferred until later. Concerning the ten pelvic fins examined by me, I may add that in eight the second mesomere bore preaxially two parameres (figs. 3 & 7); in a ninth three; in a tenth four. In most cases two postaxial rays were present (fig. 7). One fin, interesting beyond this, bore (fig. 2, right hand, as drawn) preaxially two rays, postaxially four, that being a precise reversal in duplicate of the condition observed by Schneider. In no case have I observed the distribution recorded by him.

The parameres of all the fins alluded to were, for the most part, rod-like and segmented; but in not a few instances they were branched or otherwise modified (*cf.* figs. 1, 5, 7). Reflection upon the facts recorded concerning them, to say the least, shakes our trust in the supposed regularity of their distribution. That, however, can no longer be asserted, in view of the truly remarkable condition of one pair of fins, which belonged to a fish in all respects normal and healthy (fig. 2). Günther first directed attention to the sickle-shaped contour of the *Ceratodus* fin, and all subsequent observers are agreed as to the asymmetry of its two lobes. Schneider states (23, p. 521):—"das zweite Glied des Hauptstrahls zerfällt durch eine Längsgrube in zwei Stücke. Das eine Stück behält die Richtung des Hauptstrahls, das andere Stück divergirt mit demselben und zwar bei der Brustflosse dorsalwärts, bei der Bauchflosse ventralwärts." And further, "Die Seitenstrahlen der dorsalen Hälfte der einen Flosse entsprechen derjenigen der ventralen Hälfte der anderen." A cursory glance at the pair of fins now under consideration (fig. 2 [1]) is sufficient to show how erroneous is this deduction. That Schneider has accurately represented the facts for the animals at his disposal, I have no doubt; but that his conclusions are incapable of a wider application is here proven.

[1] I was at one time under the impression, from an examination of Davidoff's figures (7, pl. 9. figs. 6 & 7), that he had been dealing with a similar pair of fins; but I am no longer in doubt. His drawing of the fin-skeleton of fig. 7 is not in accord with the description given, as regards the pelvis and basal mesomere. He, moreover, states emphatically (p. 127), "die Zahl der ventralen resp. medialen Reihe [referring to the parameres] entspricht genau der Zahl der Gliedstücke des Stammes, während diejenige der dorsalen resp. lateralen Reihe fast genau um das Doppelte grösser ist?"

Fig. 2 represents the ventral aspect of the pair of fins afore named, as they lay in life. They were attached to the pelvic cartilage (*pl.*) by a fibrous buffer, identical with that described by Davidoff (7, p. 124). The free end of the hip-girdle terminated in front in a pointed extremity (*processus impar* of Davidoff), which, as already observed by Günther (14, p. 535) and that author (7, p. 124), was bent towards the left side. I figure this (fig. 2 *a*), as its distortion is here much more marked than in any specimen yet drawn.

According to Schneider (23, p. 521) "Die Curve, welche der dorsale Rand jeder Flosse beschreibt, ist verschieden von der Curve des ventralen Randes. Nun ist der dorsale Rand der einen Flosse congruent mit dem ventralen Rande der anderen." In the specimen here figured, the two fins were sickle-shaped; the inner half of the preaxial border of the left one was straight, as represented in the figure. It will be observed that as they lay flattened out, their free ends were both directed towards the animal's right side; the excavated border, which imparts to the fin-lobe its sickle-shape, was preaxial for the right fin, postaxial for the left. When applied to the sides of the body, the apex of the former looked dorsally, that of the latter ventrally. The contour of the *Ceratodus* fin is variable; occasionally its opposite margins are symmetrical with respect to the axis; but the differences in symmetry between these two fins more than cover those which I have observed between any two members at my disposal. Turning now to the supporting skeleton, it will be seen that the second mesomere bears, as Schneider has pointed out, an accessory lobe (his "anderes Stück" referred to above). That, however, instead of being symmetrical, as he claims it to be, is, in this specimen, unsymmetrical to the utmost—for the right fin it is postaxial, for the left one preaxial. Further comment is needless, as the drawing which I give speaks for itself. Thus far the characters of the pelvic fin, as defined by Schneider, are seen to be inconstant and untenable: more than that, however; for, in that the preaxial lobe of the one fin corresponds almost to a degree (with the exception of one feature, to which I shall return) with the postaxial lobe of its fellow and *vice versâ*, there are embodied in the two the more important differences held by him to exist between the pectoral and pelvic members.

Schneider goes on to say (p. 523), "wenn man die symmetrische Stellung der vorderen und hinteren Flosse in Betracht zieht, so leuchtet die Aehnlichkeit des ersten Gliedes des Hauptstrahls mit Humerus und Femur des zweiten Gliedes des Hauptstrahls mit Ulna-Radius und Tibia-Fibula ein." I have shown above that the characters of this "zweites Glied" are inconstant for the pelvic fin. Its accessory lobe is present on that side on which the parameres are stoutest, be it preaxial or postaxial; and examination of the specimen under my hand suggests unmistakably that it has arisen as the result of coalescence between the second mesomere and the confluent bases of the two proximal parameres. The well-known lobe of the pectoral member (*cf.* figs. 5 and 6, *mt.*), first accurately

described by Huxley (19, p. 49), to which Schneider likens that of the pelvic fin, is constant in its relationships and invariably post-axial. I emphatically deny that structural similarity of the second mesomere of the fore and hind fins suggested by him, while I desire to lodge a protest against the unqualified assertion that (23, p. 523) "das Problem der Entwickelung von Arm und Bein, welches gegenwärtig so vielfach behandelt worden ist, wird dadurch . . . . seiner Lösung einen Schritt naher geführt."

The great variation here demonstrated in the relative number and calibre of the parameres of opposite sides of the normal pelvic fin at least shows that the numerical differences existing between them and those of the so-called irregular fin described at the outset are insignificant. What now of the "branching," to which attention was originally directed by Haswell (15, p. 7)? In the fin furnished by him all the rays not indicated in the drawing (fig. 1) are simple and unbranched, though somewhat unusually elongated. Many of them are transversely segmented. The question resolves itself into this—Can the irregularities represented in fig. 1 as it stands be shown to exist in a more normal fin? Bifurcation of the terminal portion of one or more parameres is no exceptional feature. Günther (14) and Davidoff (7) have both described it for the pelvic fin, and I figure an example (fig. 7) in which it had attained a marked development. Fig. 5 shows that it is no new peculiarity for the pectoral fin also[1]. I have seen a dichotomy of the pectoral paramere in one other case, and that in a fin in all other respects normal. The transverse segmentation of the axis of Haswell's fin (fig. 1) is not a whit more remarkable than that of fig. 7; while in the fin there represented, as in the pectoral one of fig. 5, irregularities of the preaxial parameres existed which far exceed in abnormality (if such it may be termed) anything forthcoming in the first-named specimen. Briefly stated, Haswell's fin differs most conspicuously from that of the more constant type in respect to the longitudinal cleavage of the axis. This phenomenon has already been recorded by Haswell, and that in a fin which recalls the one here described (15, pl. 1. fig. 6). Albrecht has figured and described (Sitzungsb. d. könig. preuss. Akad. Berlin, vol. xxxii. p. 545, 1886) a specimen of *Protopterus* (*P. annectens*) in which the distal half of the axis of the left pectoral fin had similarly bifurcated[2].

Haswell (15, p. 8), commenting upon the "branching" process which he first described, asserts the belief that "it is reasonable to

[1] I found, on examining this specimen minutely, that many of the parameres terminated in small nodules such as are represented at *. On comparison with the other specimens dissected by me, I am convinced that similar terminal segments existed in two cases, but that, owing to their delicate nature, they had been for the most part torn away in the process of dissection. The free ends of the rays from which they had been thus removed presented a characteristic truncated appearance, identical with that represented in some of the rays so carefully drawn by Davidoff (7). Putting all together, I incline to the belief that the terminal nodules in question are of fairly general occurrence.

[2] The deductions which he has drawn from the study of this fin appear to me no less unwarrantable than those of Schneider alluded to above.

regard it as an instance of atavism, and so pointing back to a pre-existing condition in which the fin-skeleton consisted of branching jointed cartilaginous elements supporting a cutaneous expansion considerably broader than that of the fin of the living *Ceratodus forsteri*." If, as therein suggested, the typical paramere has arisen from a confluence of branching-elements, such as exist to-day among some Elasmobranchs, and if it be that the mesomeres have been formed by the fusion of the basal ends of the parameres as they now stand, each mesomere would be morphologically double, and the longitudinal cleavage of this axis would thereby receive an intelligible interpretation. I am doubtful as to the probability of such a process having been involved, but, in the absence of any data upon the development of the fin, I put forward the suggestion as a possible means of accounting for the apparent irregularity. In support of this conception of the origin of the parameres, it may be stated that their reduction in number is proportionate to the thickening of the fin border. Schneider says (23, p. 521) that " die Seitenstrahlen der dorsalen Hälfte der einen Flosse entsprechen derjenigen der ventralen Hälfte der anderen." I find, however, that when (as in the left-hand fin of fig. 2—right-hand one of the drawing) that lobe which is generally thickened remains thin, its supporting rays are more numerous and of smaller calibre than usual. When, on the other hand, as was also the case in the fin represented, the usually thin lobe becomes thickened, its supporting rays get less numerous in proportion as they become more powerful. Stated otherwise, these facts go far to prove that the thickening of one or other of the fin-borders is mainly due to confluence and subsequent increase in calibre of the parameres. Suggestive, indeed, in view of all this is the occasional bifurcation of a linear series of postaxial parameres, such as is represented in fig. 7.

Perusal of the foregoing pages will show conclusively that Haswell's " branching " fin is, when compared with those of a number of other individuals, little, if at all abnormal. There yet remains for consideration that cartilage (*r*, fig. 1) which, as I have stated, is connected with the proximal mesomere ; and it has now to be inquired if a representative thereof is forthcoming in a more typical fin. After long searching I found an unmistakable representative of it, and that in none other than the left fin of the remarkable pair represented in fig. 2. Fig. 3 is a drawing of the upper third of the same. The postaxial lobe was supported, as has been already stated, by a series of delicate parameres, of which there were two to each of the ray-bearing mesomeres figured, with the exception of the first and third (*cf.* fig. 2). The preaxial lobe was, contrary to the general rule, supported by a series of larger and more powerful parameres ; of these there was one to each of the above-named segments, with the exception of the first. None of the parameres showed the slightest trace of branching.

Proximally to the postaxial rays there lay the cartilage, *r*, of fig. 3. This element was relatively far smaller than was that of the

specimen first described (fig. 1), and its relationships to the basal mesomere were the less definite of the two. It was here segmented into two pieces, while it was much more intimately connected with the two adjacent parameres than was the case in the former example. These two fins (figs. 1 and 3) stand alone, among those which I have examined, with respect to the great increase in number of the parameres of the postaxial lobe, and that also bears the cartilage now in question. If, as Haswell suggests (15, p. 8), this duplication of rays is reversionary to a "a pre-existing condition in which the fin-skeleton consisted of branching, jointed, cartilaginous elements," the only conclusion which seems to me justifiable is that the appearance of this new element amounts to that of the reappearance of one which has been lost. Haswell has described an individual (15, figs. 6 and 7) in which the cartilage in question appears to have been present on both sides; and it is instructive to remark that in both fins the rays of the postaxial series were, as with my specimens, the more numerous. I have already stated that in the fin described at the outset (fig. 1), the whole skeleton was, with the exception of the bar in question and the basal mesomere, very slight and leaf-like. This simplification of structure, so suggestive of the reversion claimed by Haswell, is seen in the basal mesomere itself. That was (fig. 1, *m.p.*) much thinner and more flattened than is usual, and it bore but one processus muscularis (*tb.*) instead of the three described by Davidoff (*cf.* 7, pl. 8). All the foregoing facts point to the conclusion that the newly described cartilage exists only in fins whose postaxial rays remain little modified. There is, therefore, good reason to regard it, let its homology prove to be what it may, as atavistic. It has disappeared in the normal fin, under a confluence of the parameres of its own side, and a consequent thickening of the postaxial fin-lobe.

### III. *The Pectoral member of* Ceratodus *compared with the Pelvic one of the same and the Pectoral one of the Plagiostomes.*

Haswell, reviewing (15, p. 5) the well-known observations and hypotheses of Balfour (1), Thacher (24, 25), and others, which led them to dissent from the interpretations of Gegenbaur and Huxley, says that they, together with the facts which he brings forward, seem to place it beyond a doubt that the limb of *Ceratodus*, "so far from representing a primitive and generalized type, is, as, indeed, we should expect from various other points in the organization of the animal, in reality highly specialized, and to be regarded as derivable from such simple limb-skeletons as those of the *Selachii*." In this he was anticipated by Balfour (1) whom he quotes. Balfour wrote (p. 669), when criticizing Huxley's position, the leading tenets of which he supported so far as the identification of the chief constituents of the fin-skeleton go, "I should be much more inclined to hold that the fin of *Ceratodus* has been derived from a fin like that of the Elasmobranchs, by a series of steps similar to those which Huxley supposes to have led to the

establishment of the Elasmobranch fin, but in exactly the reverse order"[1].

The researches of Huxley and Balfour have proved that the propterygium of Gegenbaur (figs. 9 and 10, *pt.*) represents, throughout the Elasmobranch series, but one or more preaxial rays. It is the most variable of the three basal elements of the Shark's fin, and most observers are now agreed as to its morphological unimportance. The above-named writers are further at one in their estimate of the morphological value of the Elasmobranch meso- and metapterygia (*ms.*, *mt.*, figs. 9 and 10). That they disagree, however, upon at least one vital issue is well known, and the balance of opinion holds to-day that the solution of the 'archipterygium' question is to be sought in a reconciliation between their views.

Huxley has described and figured (19, p. 48) the maximum development yet observed for the so-called propterygium of the *Ceratodus* pectoral fin. That structure cannot be definitely recognized in the pelvic fin. The determination of Huxley (19), Balfour (1), and v. Rautenfeld (22), which regards the axis of the *Ceratodus* fin as the mesopterygium, is too familiar to call for comment here. It must suffice to state that I accept it in the main, if not wholly, and assume for the present that the entire axis has the value which Huxley first assigned to it.

It is at this point necessary to discuss, more fully than heretofore, the nature of the differences between the pectoral and pelvic finskeletons of *Ceratodus*. Schneider has asserted (23, p. 521) that "die Seitenstrahlen der dorsalen und ventralen Hälfte der Flossen sind ungleich," also that the "Seitenstrahlen der dorsalen Hälfte der einen Flosse entsprechen derjenigen der ventralen Hälfte der anderen." There is an undoubted tendency towards the assumption of the condition which he thus formulates for *Ceratodus*, and it seems to me probable that a common determining cause may have led up to it and the condition realized in *Protopterus* (*cf.* Schneider, p. 524); but the definition no longer holds invariable for the former animal, in view of the facts thus far adduced. I have already stated that the presence of one preaxial paramere in connexion with each mesomere is a constant character of the *Ceratodus* pectoral fin, and I turn now to the distribution of the postaxial rays. I have given on p. 7 the average distribution for eight pectoral fins examined. The minimum observed was, taking the mesomeres in order of succession from within outwards, 3 . 1 . 2 . 1, the maximum 4 . 2 . 2 . 2. In no case have I observed five rays in attachment with the second mesomere, as stated by Schneider. Of the eight specimens examined, the second mesomeres of five bore each three rays; the third and fourth of seven each two; and the fifth of six each one. It is thus certain that variation in the distribution of the postaxial parameres (*cf.* fig. 6) is, beyond doubt, far

[1] Günther originally advanced a somewhat similar opinion (14, p. 534), but he conceived of the process as having gone on along lines as yet incapable of support.

less marked than with the pelvic member; but the fact which stands out most clearly is that the second mesomere invariably bears the greatest number of these rays. They are carried (figs. 5 and 6, *mt.*) upon a special lobe of the axial cartilage ("das divergirende Stück" of Schneider) already alluded to. The free border of this lobe slopes, in every case examined by me, gradually towards the proximal mesomere (*m.p.*), and it is, moreover, in all, marked off from the body of the second mesomere by a deep furrow (indicated in the figs. by a dotted line).

I now proceed to discuss its homology, and having arrived at the conclusions to be formulated in the sequel through a comparison with the pectoral fin of *Cestracion*, I pass at once to the consideration of that.

Gegenbaur and Huxley are both agreed that the base of the *Cestracion* fin is supported by two cartilages (fig. 10) held by them to represent the mesopterygium (*ms.*) and the metapterygium (*mt.*) of other Selachians. Most recent writers have adopted their views (*cf.* Hubrecht and Sagemahl in Bronn's 'Klassen und Ordnungen des Thier-Reichs,' vol. vi. part 4, Pisces). Huxley, instituting a comparison (19, p. 50) between the corresponding fins of *Cestracion* and *Notidanus*, regards them as representative of the transition stages in the shortening of the *Ceratodus*-like "archipterygium," by which he concludes the typical fish-fin has arisen. Gegenbaur (9, p. 148) likens the *Cestracion* fin to that of *Acanthias*, and says "das Propterygium fehlt gänzlich."

Huxley, holding further that the propterygium (preaxial ray) of *Cestracion* is removed from the shoulder-girdle, as in *Ceratodus*, asserts that in *Scyllium* (pp. 50–52) "the further shortening of the axis gives rise to still greater changes. The axial cartilage (*mesopterygium*) is relatively small; but the enlarged postaxial cartilage (*metapterygium*) has extended upwards along the postaxial face of the first, until it has not only reached the articular surface of the pectoral arch, but furnishes a large part of the articular cavity. In like manner the proximal preaxial ray (*propterygium*) has ascended along the preaxial face of the axial cartilage, until it also is able to furnish a facet which completes the anterior part of the cup for the condyle of the pectoral arch." He holds therefore that the pectoral fins of *Notidanus*, *Cestracion*, and *Scyllium* represent, in the order enumerated, the successive steps in the modification alluded to above, and he, in accordance with the statements quoted concerning the propterygium and metapterygium, relegates the two former fins to his category of the "unibasal" type, as distinguished from that of the latter animal, which he holds to typify the "tribasal" one predominant among the Plagiostomes (*cf.* table which accompanies his essay).

From an examination of the fins of two young Cestracions, I can state without further hesitation that the mesopterygium of the adult is (as Mivart has suspected, 21, p. 477) a compound of the pro- and mesopterygia. Fig. 9 represents one of the fins referred to. The animal died at the period at which the two (*ms.* and *pt.*)

were beginning to unite. The propterygium (*pt.*) is seen to compose fully the anterior third of the whole mass, its base being made up of two segments, the proximal one of which contributes nearly half the articular cup, entering at least as fully into the formation of the same as does its representative in *Scyllium* (*cf.* Huxley, 19, p. 48, fig. 10). In the adult fin (fig. 10) the original boundary line between the pro- and mesopterygia is represented by a groove indicated in Huxley's figure (here reproduced) by a dotted line.

The pectoral fin of *Cestracion* is thus shown to conform to the Selachian type, being identical most nearly with that as represented by *Acanthias* (*cf.* Gegenbaur, 9, pl. 9. fig. 4, and Mivart, 21, pl. 77. fig. 2). *Cestracion* must, on the evidence now forthcoming, relinquish its position in the series established by Huxley; it must, to say the least, change places with *Notidanus*. The main articulation of the fin of the last-named fish is established, as is well known, through the agency of the mesopterygium. Gegenbaur originally described a basal preaxial bar in *Notidanus*, and he homologizes it (9, p. 140) with his propterygium. This enters, if anything, more fully into the articulation with the shoulder-girdle than does its representative in *Cestracion*. There is connected with its distal end, in *Hexachus*, a smaller piece (*cf.* Gegenbaur, *op. cit.* pl. 9. fig. 1) which appears to represent the second segment of *Cestracion*, reduced, as an outcome of the great expansion of the front border of the mesopterygium. Mivart has suggested (21, p. 444) that the mesopterygium represents a coalescence of the pro- and mesopterygia; but I am inclined, upon careful examination of the specimen under my hand, to dissent from that view.

The metapterygium of *Notidanus* enters into a feeble but definite connexion with the pectoral arch, such as is not the case in *Cestracion*. That the fins of these two genera differ from those of some of the Sharks is indisputable, but they do so to an insignificant degree, incapable in itself of supporting the "unibasal" type; that, in face of the facts here adduced [1], rests upon an insufficient basis.

Returning now to *Ceratodus*; the lobe which, in the pectoral fin, carries the 3–5 proximal postaxial parameres (figs. 5 and 6 *mt.*) is, as has been stated previously, marked off from the adjoining mesomere by a deep furrow.

Günther observes (14, p. 532) that the conjoined mass shows, in "horizontal section," lines of "the former divisions" into what he holds to correspond to the "three carpals" (pterygia) of most Plagiostomes. This has been denied by Huxley (19, p. 47). Setting aside this difference for the moment, I desire to call attention to the similarity of the furrow described above to that which

[1] When, moreover, it is considered that in the pectoral fin of *Polypterus*, which Huxley relegates to the "tribasal" category, the mesopterygium is (as Gegenbaur pointed out, 10, p. 139) excluded from articulation with the limb-girdle, the statement that (p. 55) "the mesopterygium is the proximal piece of the axial skeleton, which constantly retains its primary articulation with the pectoral arch," must needs be modified.

marks off the propterygium from the mesopterygium in the adult *Cestracion*. On a comparison of the two, I submit, with some degree of confidence, the opinion that the postaxial lobe of the second mesomere of *Ceratodus* (figs. 5 and 6, *mt.*) is the homologue of the Elasmobranch metapterygium. Comparison of that lobe and its attached rays (fig. 6) with the metapterygium of *Cestracion* and its rays (fig. 9) reveals a striking similarity, even in detail, between the two. Did the metapterygium of the Shark unite, as does its propterygium, with the axial plate *ms.*, it would be difficult indeed to find a distinction between the first named and that which, in *Ceratodus*, I claim as its homologue.

The homology which I here seek to establish bears out, with certain modifications, Balfour's view cited that "the fin of *Ceratodus* has been derived from a fin like that of the Elasmobranchs." That observer first recognized (1, p. 668) that the metapterygium (his *basipterygium*) is morphologically the most important and, phylogenetically, the most primitive of the basal elements; while he suspected (*ibid.*), but did not demonstrate the fact, that that structure is formed by the coalescence of rays. Huxley had already asserted this belief, in dealing with the metapterygium of *Notidanus* (19, p. 50), which he regarded as being "formed by the coalescence of the axial ends of the postaxial rays" (presumably on the shortening of the fin axis). Dohrn has recently substantiated the deductions of Thacher, Mivart, and Balfour under this head, in having found that the metapterygium is (8, p. 174), in both pectoral and pelvic fins of the Shark, like the basal bar of the median fins, made up of "unpaare Knorpelstrahlen, die anfänglich oder jede Verbindung mit anderen Skelettelementen bleiben." He reiterates the statement on p. 182 in the words "was als Basipterygium beschrieben ist, stellt nur die verschmolzenen, wei sehr nah an einander leigenden, Basen der Flossenstrahlen dar und existirt nicht unabhängig von diesen."

In face of the above facts, my view demands that a primary distinction shall be demonstrated between the second pectoral mesomere in *Ceratodus* and that lobe which I hold to represent the metapterygium. In Günther's original specimen (fig. 8) the said lobe was not represented in that which is now known to be its typical form, while the rays (*r*) which are usually attached thereto were for the most part independent. The proximal two of these appear to have been somewhat smaller than usual, but it is highly interesting to note that the two distal ones were uniting at their bases to form a plate-like structure (*mt.*) which showed no signs of confluence with the adjacent mesomere. This plate corresponds in its mode of origin with the metapterygium (basipterygium of Balfour), as defined by the above-named authors, and, in its relationships to the rest of the fin-skeleton, with the lobe now under consideration. I regard its condition as there represented to be indicative of the primary independence which my interpretation necessitates.

Günther goes on to say (p. 532) that he found "lines of the former divisions" of the second mesomere of this specimen preserved, in the shape of tracts of white connective tissue. Huxley

denies the existence of these, as has previously been stated; but let them be present or not, it is certain, should Günther's observation hold good, that they cannot indicate the original lines of separation between pro-, meso-, and metapterygia, as now understood.

## IV. *On the proximal Postaxial Elements of the* Ceratodus *Pelvic Fin.*

The cartilage which I have already described (figs. 1 and 3) as directly connected with the postaxial border of the basal mesomere of the *Ceratodus* pelvic fin is ray-like, but relatively powerful, in one of the two specimens (fig. 1). In the other (fig. 3) it is altogether smaller and segmented into but two pieces, instead of into three, as in the former specimen. While it here meets the distal end of the proximal mesomere, it is much more intimately connected with the second piece of the axis than in the former specimen; but on the supposition that the cartilage is homologous in both fins, its condition in fig. 3 is precisely that which would result from a further reduction of that of fig. 1, such as there is good ground to believe, for reasons previously alleged, has actually gone on. In the second specimen the cartilage in question is further interesting, in that it bears one and is in close connexion with a second of the proximal parameres.

In the specimen figured by Günther (14, pl. 36. fig. 4) already referred to (p. 5), the proximal piece of the axis bears two cartilages. Fig. 4 is a reproduction of his drawing. The distal cartilage is ray-like, and stands related to the base of the proximal mesomere as does an ordinary postaxial paramere to the corresponding border of a typical mesomere. The proximal cartilage appears to have been free of the basal piece altogether. It is, as shown in the figure, plate-like, and I have little doubt but that it was formed by the confluence of the basal ends of at least the two rays which it carries. These skeletal elements, as they stand in Günther's specimen, combine the characters of those of the two described by me (figs. 1 & 3). The postaxial parameres are, as in my specimens, much simpler than usual, and the whole series of lateral rays are in his fin more uniformly distributed than in general. The basal plate is (fig. 4, *mt.*), like the corresponding bar of fig. 1, in near relationship with the proximal mesomere, although but loosely connected therewith; while it agrees with the corresponding element of fig. 3 in giving attachment to a couple of rays. Comparing the proximal postaxial elements of my two specimens and Günther's figure with the corresponding region of the pectoral fin-skeleton, and reflecting that the typical metapterygium is formed by a confluence of the basal ends of the rays of that region, I incline to the belief that the vestiges in question represent that lobe of the fore limb which I claim as the metapterygium, together with its associated rays.

Should the cartilages now under discussion have the morphological value which I am seeking to establish for them as probable, the well-known views of Gegenbaur (10, 11), and Huxley (19) will

receive refutation, proportionate to the support furnished for those more especially of Balfour, Haswell, and Dohrn already cited.

As stated previously, the cartilage *r* of fig. 1 is ray-like, but stouter and more powerful than that of any ordinary paramere.

In seeking light on this question, one naturally turns to *Polypterus*, the affinities between which and the *Dipnoi*, originally pointed out by Huxley (18), have nowhere been denied. The *Polypterus* pectoral fin is, as is well known, supported upon three basal elements. The mesopterygium (fig. 11, *ms.*) is held by all to represent that of the Plagiostomes, and no one has yet challenged Gegenbaur's determination (9, p. 148) of the homology between the elongated postaxial bar (*mt.*) of this fish and the metapterygium of the *Plagiostomes* and *Chimæroids*. Huxley says of this fin (19, p. 53) that "the Scyllium type is essentially preserved." Comparison of the *Polypterus* pectoral fin (fig. 11) with the pelvic fin of *Ceratodus* represented in fig. 1 would appear at first sight to suggest a homology between the basal postaxial bar (*r*) of the latter and the metapterygial bar (*mt.*) of the former. If this be justified, it would further appear, accepting the homology of the metapterygium of *Polypterus* with that of the *Elasmobranchii*, that the two fins might have been derived along a line of modification characterized by the assumption on the part of the metapterygium of a ray-like character, and by the subsequent elongation of the mesopterygial plate (*ms.*). The probable truth of the latter assertion seems to me very great indeed. The mesopterygium is, in *Polypterus* (fig. 11, *ms.*), already elongated beyond the limits met with elsewhere, displacing in the process the marginal rays. Continue that elongation, and there could only result a *Ceratodus*-like product. As concerns the former supposition, however, comparison of the fin-skeletons represented in figs. 1, 3, & 4 is sufficient in itself to show that the proximal postaxial ray of fig. 1 most probably represents the distal one of those related to the proximal mesomere of fig. 4. Comparison of the latter (fig. 4) with the proximal end of the pectoral fin of the same side of the same animal (fig. 8) shows unmistakably that in the plate-like structure resulting from the fusion of the basal ends of the two proximal parameres we have to deal with the last trace of the metapterygium, defining that, as must now be done, as a product of the confluence of the inner ends of the proximal postaxial rays, the distal ray being, from the nature of its relations therewith, one of the same series.

Consideration of the above facts renders the homology of the supposed metapterygium of *Polypterus* somewhat doubtful. Gegenbaur, when pointing to the same, realized the similarity between both pro- and metapterygia so-called by him (fig. 11, *pt.* and *mt.*) and the marginal rays[1]. He at first suggested (10, p. 139) the possibility that the exclusion of the mesopterygium from connexion with the

[1] The difficulty of interpretation of the supposed propterygium is greatly increased by the presence of the cartilage marked * in fig. 11,—by no means the least puzzling element in this fin. As will be seen, it is grafted upon the anterior border of the propterygial rod; from it, however, it is perfectly distinct in

shoulder-girdle may have been due to a displacement of the same by two rays. Should this be so, the metapterygium must there have disappeared, as from the *Ceratodus* pelvic fin, under the corresponding enlargement of the mesopterygial plate. The only alternative view possible is that the metapterygium does represent that of the Elasmobranchs. If this be so, comparison of the pectoral fin of *Polypterus* (fig. 11) with that of the Plagiostomes, as represented in *Scyllium*, where the mesopterygium is relatively small, would seem to show that the loss of connexion between the metapterygium and its rays has been to no small extent due to a displacement of the latter by the elongation of the expanding mesopterygium, no less than by the simplification in structure of the metapterygium itself. The last step in the former process would appear, indeed, to be retained in the living *Polypterus* (** fig. 11).

In the absence of embryological data further discussion of this difficulty would be fruitless. It is much more pertinent to observe that in both *Ceratodus* and *Polypterus* the initial step in the modification has been, in any case, one of elongation of the mesopterygium, and evidence has been adduced to show that in the *Dipnoi* (if not in *Polypterus* also) the metapterygium has been thereupon reduced and finally suppressed. The only traces of either it or its rays yet recorded in the *Ceratodus* pelvic member are forthcoming in fins whose postaxial parameres are more numerous and less specialized than is generally the case. If this simplification in structure of the most specialized portion of the pelvic fin-skeleton is, as I have attempted to show, reversionary to a condition which has been lost, the characters of those elements which reappear under the simplification, when compared with those to which they most nearly correspond in the pectoral fin, go far towards bearing out the presumed origin of the *Ceratodus* fin from a primarily expanded predecessor.

### V. *On the Morphology of the Axis of the* Ceratodus *Fin.*

The entire axis of the *Ceratodus* fin is held by Huxley (19) Balfour[1] (1), and v. Rautenfeld (22) to represent an elongated

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the two specimens examined by me. It has been figured by Wiedersheim (29, p. 199), but I have been unable to find a description of it. I think it not improbable that it may have been derived from the mesopterygium, the closely related lower anterior end of which may (as Wiedersheim has shown) insert itself between the supposed propterygium and the marginal rays. In the absence of embryological data further discussion of it would be useless.

[1] Baur has recently called attention (3, p. 6) to the fact that Gervais has priority over Humphrey in the enunciation of the hypothesis that the paired fins are dismembered portions of a lateral fold. Gervais writes (12):—"Si l'on considère que les rayons des nageoires impaires des poissons ont une analogie incontestable avec ceux dont la réunion formes les nageoires paires des mêmes animaux, c'est à dire leurs membres véritables, on est naturellement conduit à se demander s'ils ne seraient les homologues de ces derniers, et si l'état d'isolement dans lequel ils restent les unes par rapport aux autres, ne résulterait pas de ce que chacun d'eux ne conserve pas complètement ses rapports avec celui des segments osteodesmiques dont il est tributuire. Alors on pourrait les

mesopterygium, and by Gegenbaur (11) to represent the metapterygium. The points of difference between the two sets of observers are so well known that recapitulation of them would be superfluous here. I incline most nearly to Huxley's view, and hold that the axis represents mainly, if not wholly, the mesopterygium of the Sharks; but I regard its condition in the latter as typical of its earlier and more primitive state. I moreover think it not unlikely that the short-lobed fin of the *Crossopterygidæ* will prove to be of an earlier type of structure than that of the elongated one of the living *Dipnoi*. Extended observations along the lines already laid down by Traquair, in his Monograph on *Tristichopterus* (27), are greatly to be desired. That the elements described by him are probably, and that those described by Goldfuss (13) and Kner (20) in *Xenacanthus* are certainly, homologous with those of the axis of the *Ceratodus* fin, I fully believe, and we have here the foundation of a line of study which must soon yield fruitful results[1]. Wiedersheim is the only worker who, to my knowledge, has offered an opinion upon the last named. He says (29 p. 195), speaking of the *Ceratodus* fin, "dass dieser Organisationsplan der Brustflosse auch bei untergegangenen Fischgeschlechtern eine Rolle gespielt haben muss, steht unzweifelhaft fest und ich möchte dabei nur an den aus der Permformation stammenden *Xenacanthus decheni* erinnern."

There can no longer be much doubt that the confluence so frequently seen between one or more rays and the mesopterygium of the Elasmobranchs represents the last trace of the process by which that structure is formed (*cf.* Dohrn, cited on p. 15). This granted, it becomes a question as to how far the axis of the *Ceratodus* fin, as here defined, represents a further extension of this fusion of primarily parallel rays or an elongation of the mesopterygial plate, as it exists in the Sharks. The fact that irregularity in distribution of the parameres is generally accompanied by that of the segmentation of the axis in *Ceratodus* (*cf.* especially figs. 1, 5, & 7), shows that there is an intimate connexion between the two; and this is the more obvious on reflection that Davidoff has shown (7, p. 145) that the segmentation of the axis does not stand in constant relationship to the muscular attachments[2]. It is moreover inconceivable, if

regarder comme autant de rayons membraux restés libres, et ils seraient les homologues de ceux qui, par leur asservation, donnent naissance aux membres proprement dits sur d'autres points du corps."

[1] I look with great satisfaction upon the work now being done in this direction by Smith Woodward (*cf.* P. Z. S. 1886). It is time that some such check should be kept upon the deductions of the embryologist (*cf.* Baur, Morph. Jahrb. vol. viii. p. 453).

[2] He writes, "Da wir auch an der Muskulatur eine den einzelnen Segmenten der Stammreihe entsprechende Gliederung fanden, zo gewinnt diese Ansicht an Wahrsheinlichkeit, obwohl immerhin noch einzuwenden ist, dass die physiologische Bedeutung dieser Gliederung eine nur äusserst minimale sein kann, dass ferner auch die Zwischensehnen der Stammuskulatur in gar keiner näheren Beziehung zu den Segmenten der Stammenreihe stehen." I could find no difference between the muscles of the fin represented in fig. 6 and those described by him.

the *Ceratodus* fin has arisen as an elongation of a primarily expanded predecessor, that such a fusion of the approximated ends of the rays could have resulted from that simple process. I am of opinion that the distal portion of the mesopterygium of *Ceratodus* has arisen on an elongation of a pre-existing plate, by a process such as is seen at its earliest phase in *Polypterus*.

A difficulty, however, arises with respect to the basal mesomere of *Ceratodus*, which, if it represents the proximal end of the mesopterygium, differs from that of all other fishes in forming (in the pectoral fin, at any rate) the sole support for the base of the fin. Gegenbaur, who has paid considerable attention to this matter, at first acquiesced (10) in Huxley's belief in the close relationship between *Polypterus* and the *Dipnoi*. Commentiug upon the pectoral fin of the former animal, he writes (p. 138) "ausser den Selachiern bei denen die zweieilige Form des Archipterygium in die einzeilige übergeht, besitzt vielleicht nur noch *Polypterus* unter den lebenden Ganoïden das primäre Archipterygium im Flossenskelete." He goes on to advance the view that the fin of *Polypterus* represents a shortened-up derivative of the *Ceratodus* type; but finally he reverts to bis original position, holding, chiefly on account of the loss of connexion between the mesopterygium and shoulder-girdle, and of the great structural difference between the pectoral and pelvic fins, that (p. 140) "demnach kann ich das genannte Skelet von *Polypterus* nicht unmittelbar auf das primäre Archipterygium beziehen, sondern leite es, wie jenes der anderen lebenden Ganoïden, von der secundären, nur *eine* Reihe von Radien besitzenden Form ab."

The pelvic fin of *Ceratodus* appears, at first sight, to be exceptional in the possession of a well-developed mesopterygium. Davidoff has brought forward good evidence to show that the element hitherto regarded among *Ganoids* and *Teleostei* as the pelvic girdle is (5. p. 125, and 6. p. 433) homologous with the basal piece of the *Ceratodus* fin, and he terms it the basal segment of the metapterygium. He has shown good reason for believing that the true pelvis is seen for the last time among the *Osteichthyes* in *Polypterus*, where it is represented by two or three vestigial cartilages (*cf.* 6. p. 462, pl. 21, and Wiedersheim, 28) lying immediately in front of the applied ends of the basal pterygia of opposite sides. Upon careful consideration, I am disposed to accept his interpretation as it applies to the Ganoids and Teleostei, but I am more dubious about it as applying to the Dipnoi.

Examination of either of the paired fins of *Ceratodus* in relation to the limb-girdle appears, at first sight, to favour Huxley's view that the whole fin-axis answers to the Selachian mesopterygium. If this be so, that element must, in elongating, have carried down with it the metapterygium, and the propterygium if present.

Balfour, criticizing Huxley's view that the basal mesomere is the proximal piece of the axial skeleton of the limb of *Ceratodus*, says (1, p. 669), "The entirely secondary character of the mesopterygium and its total absence in the young embryo *Scyllium* appear to

me as conclusive against Huxley's view, as is the character of the embryonic fin against that of Gegenbaur."

Examination of the pectoral fin of *Ceratodus* shows that the elements which I hold to represent the metapterygium and its rays (figs. 5, 6, & 8, *mt.* & *r.*) are related to the postaxial border of the second mesomere. There is at most a bare suggestion of a relationship to the proximal mesomere (*m.p.*). In the hind limb this is otherwise, for those parts of the skeleton which most nearly repeat the characters of the presumed metapterygium of the fore limb are unmistakably connected (figs. 1 & 4) with the proximal mesomere. If they really represent the metapterygium and its rays as they occur among the lower fishes, it is, I think, not unlikely, putting together these facts and those recorded by Davidoff, that while the metapterygium has for the most part disappeared, the proximal mesomere may, after all, turn out to represent the proximal end of that structure as defined by Huxley, early differentiated and segmented off.

The above suggestion, should it be substantiated, would explain the fact that the proximal mesomere of *Ceratodus* is the only constituent of the fin-axis whose characters are constant. It would simplify our conceptions of the fins of the Ganoids and Dipnoi, and bring into harmony the supposed divergent modifications of the fins of opposite extremities; while it would show the pelvic member to be, on the whole, less modified than is usually thought. I am disposed to think, moreover, that it receives support from the absence of preaxial rays in connexion with the basal mesomere of *Ceratodus*; from the complete exclusion of the mesopterygium from connexion with the shoulder-girdle in *Polypterus*; and from the condition of the pelvic fin of that animal, already alluded to, no less than from the marked tendency towards an increased development of the proximal end of the pectoral metapterygium among the living *Ganoids*.

Still more suggestive is the condition of the basal elements of a *Protopterus* pectoral fin represented in fig. 8 *a*. Wiedersheim has (as I have already mentioned, p. 5) shown that the proximal piece of the pectoral fin-skeleton of this animal bears ray-like elements. He describes a smaller distinct ventral (postaxial) one and a larger dorsal (preaxial) one, which is confluent with the main piece (proximal mesomere as compared with *Ceratodus*). I have examined two specimens; in one of them the latter is much smaller than in his example, while in the other (fig. 8 *a*) there is no trace of it. I can only conclude therefore that it is a lobe of the basal mesomere, variable in character. Not so with the former; that is in both perfectly distinct, being separated from the basal mesomere by a fibrous tract, such as subdivides any two segments from each other. In that specimen which was destitute of the preaxial process (fig. 8 *a*) its characters are still further noteworthy. It is elongated and shows traces of subdivision into two pieces, the basal one of which is swollen and enlarged in common with the proximal mesomere (*m.p.*), and from that it appears most clearly to have been derived. The second segment of the axis is in relation with both the proximal

mesomere and the swollen basal piece referred to; and the whole condition of the parts is such as would have resulted did the proximal mesomere and its related lateral elements represent a shortened-up metapterygium.

Beyond this, the pelvic member of *Ceratodus* differs most conspicuously from that of the Plagiostomes and Osteichthyes in the presence of an elongated mesopterygium. Balfour first showed (1, pp. 666–7) that the development of the pelvic fin of the Shark is arrested at a comparatively early stage. He and subsequent writers regard the enlarged preaxial ray, which Huxley would hold to represent the mesopterygium, as the propterygium. He has also called attention to the fact that the mesopterygium is not there represented; and the only anticipation of that structure forthcoming among the Plagiostomes, known to me, is the comparatively insignificant one described by Haswell (16. p. 23, pl. i. fig. 3) for *Heptanchus indicus*.

## VI. *On the Homologies of the Chimæroid Fin-skeleton, as compared with that of* Ceratodus.

Huxley, discussing the morphology of the Chimæroid pectoral fin, insists (19, pp. 52–53) upon the close relationship which it bears to that of *Ceratodus*. The former fin is, as is well known, supported upon two basal elements, both of which are in intimate connexion with the pectoral girdle. The postaxial of these is held by all to represent the metapterygium.

As to the preaxial cartilages:—Huxley (19, pp. 52–53), whose view demands that the mesopterygium "constantly retains its primary articulation with the pectoral arch," completely reverses Gegenbaur's determination (9, p. 145), and regards the smaller basal one as the mesopterygium, and the larger ray-like distal one which it bears as the propterygium. Mivart, on the other hand, insists (21, p. 478) on the absence of the mesopterygium, and regards both preaxial elements as homologous with the propterygium. Comparison of the fin of *Chimæra* with that of the Selachians, as represented in *Hexanchus*, appears to me to warrant his view.

It is interesting, here, to recall Huxley's remarks upon the metapterygium, when dealing with *Chimæra*. Having asserted the belief that the metapterygium of *Notidanus* is "formed by the coalescence of the axial ends of the postaxial rays," he goes on to say (p. 53), "the metapterygial cartilage cannot, in *Scyllium*, at the same time represent coalesced postaxial rays, as the analogy of *Notidanus* would suggest, and the second joint of the axial skeleton as the analogy of *Chimæra* .... indicates." Did the mesopterygium exist in *Chimæra* in the form so constant among the Plagiostomes —that of a fusion of the basal ends of the rays interposed between the pro- and metapterygia—he could, in comparing the Chimæroid and *Ceratodus* fins, only have come to the conclusion formed by me (p. 15), in describing the second pectoral mesomere of the latter.

The pelvic fin of the Chimæroid is in an exceptionally interesting

condition. Its postaxial border is supported by a cartilage, admitted by all to represent the metapterygium (fig. 12, *mt.*). This appears to be produced out into a preaxial lobe, which is regarded by Davidoff (4. p. 470, pl. 28. fig. 3, and pl. 29. fig. 18), who last described it, as consisting of a single piece answering to the propterygium.

It also recalls most closely that lobe from which Balfour held (1, p. 667) that both pro- and mesopterygia are derived. In a young Chimæroid pelvic fin examined by me (fig. 12), the lobe in question is seen to be formed by the fusion of three preaxial rays, and careful examination has shown that the last traces of an original separation between it and the metapterygium (indicated in the drawing by a dotted line) exist. Did that persist, the fin would correspond in all essential respects with the pectoral member, as I have defined it; and I hold that this preaxial lobe is neither more nor less than the propterygium [1]. Mivart comments (21, p. 465) upon the "close resemblance" between the pectoral and pelvic fins of the Chimæroids. Comparing the pelvic fin of these animals (*Callorhynchus*) with the pectoral ones of *Acanthias* and *Scymnus*, he concludes (p. 456) that the basal cartilage represents, in the former, all three pterygia fused into one. The considerations put forward above, taken together with the fact that the mesopterygium never appears in the Plagiostome's pelvic fin, beyond the insignificant degree observed by Haswell, appear to me to negative this view.

The facts now under notice suggest, but do not prove, that the mesopterygium is never represented at all in the Chimæroids; and that with respect to that feature those fishes stand on a lower platform than do the living Plagiostomes. Moreover, if the preaxial cartilages of their pectoral member represent the propterygium, as I believe, an absolute structural identity is proven between the pectoral and pelvic fins of the group. Both would appear to have been derived from the fins of an ancestor in which the mesopterygium was not differentiated; and if so, that element must have been of comparatively late origin.

Davidoff has pointed to the existence of structural similarities between the hip-girdles of *Chimæra* and *Ceratodus* (7, pp. 142–3); and if the magnificent array of structural affinities between the two, so successfully demonstrated by Huxley (19), have the weight which he assigns to them, I think it more than probable, if, as I have suggested, the basal mesomere of *Ceratodus* is a derivative of the metapterygium, that the paired fins of the Dipnoi may have arisen, side by side with those of the Plagiostomes, from some such form as is to-day represented by *Chimæra*—the fusion of the rays to form the mesopterygium having gone on independently, the intercalation of that structure between the applied bases of the pro- and metapterygia, so characteristic of the Plagiostomes, having been a comparatively late process.

[1] The free ray represented at * in fig. 10 has been described by Davidoff (*op. cit.* p. 471). The spur-like outgrowth of the same, which I think may not improbably represent the coalesced vestige of a second similar one, was not present in his specimen.

If the above suggestion should prove to have weight, the condition of the basal parts of the *Polypterus* fin, in which the mesopterygium is in no way in connexion with the shoulder-girdle, can only be a lowly one.

It may not be inappropriate here to call attention to the conception lately put forward by Baur (2, p. 663) concerning the morphology of the cheiropterygium. He returns to Gegenbaur's first position, and maintains that the limb of the land-animal has been derived directly from the ichthyopterygium. In that case the *Ceratodus* fin, as it stands, can only represent the initial phase in a line of modification of the ichthyopterygium, culminating in *Protopterus* (to include *Lepidosiren*. *Cf.* Ayers, Jenaische Zeitschr. vol. xviii. p. 479, 1885, and Schneider, *op. cit.*).

Davidoff claims that the *Ceratodus* pelvic fin (7, p. 127) "trotz der Einfachheit des Ganzen, sich bedeutend komplicirter gestaltet, als bei den früher bearbeiteten Fischen." He uses the words in a physiological sense, it is true, but that in face of his concluding statement that (p. 160) "das Endergebnis aber besteht darin, dass von der Ceratodus-Extremität sich diejenige der Haie ohne Schwierigkeiten ableiten lässt." This is, in my opinion, far from proven.

## VII. *Conclusions.*

1. That the characters of the skeleton of the *Ceratodus* paired fins are inconstant, except for those of the preaxial parameres of the pectoral fin and the basal mesomere of both pectoral and pelvic fins.

2. That a metapterygium is always present in the fore limb, in a reduced condition and usually confluent with the second mesomere.

3. That traces of what appears to represent a metapterygium are occasionally to be met with in the hind limb, under conditions which point to atavism.

4. That the basal mesomere of the *Ceratodus* fin may conceivably have been derived from the metapterygium.

5. That the structural features of both paired fins of the Chimæroids are identical, and characterized by the absence of a mesopterygium.

6. That the paired fins of the Plagiostomes and Dipnoi have, in all probability, arisen independently from a type of fin most nearly represented by that of the living Chimæroids.

7. *Proven incidentally.*—That the basal cartilage of the *Cestracion* pectoral fin, usually regarded as the mesopterygium, is a compound of the pro- and mesopterygia of other Plagiostomes.

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## IX. DESCRIPTION OF THE PLATES.

### Plates I.–III.

With the exception of fig. 2, all are drawn in the same relative position. The postaxial (internal) border looks towards the left hand.

Fig. 1. A "branching" pelvic fin of *Ceratodus*. Right side, dorsal aspect. Nat. size.

2. The two pelvic fins of a second specimen. Ventral aspect. ×1½.

2*a*. The anterior portion of the pelvic girdle of the same. Nat. size.

3. The proximal third of the left fin of fig. 2. Ventral aspect. Nat. size.

4. Proximal third of a right pelvic fin; indicated as seen from the ventral aspect, for sake of comparison with figs. 1 and 3. (After Günther.) Nat. size.

5. The left pectoral fin of fig. 2. Ventral aspect. Nat. size.

6. Proximal portion of the corresponding fin of a fourth specimen. Ventral aspect. Nat. size.

7. Proximal portion of the left pelvic fin of the same specimen. Ventral aspect. Nat. size.

8. The proximal third of the left pectoral fin of a fifth specimen. Drawn to same scale as figs. 5 and 6. (After Günther.)

8*a*. Basal portion of a left pectoral fin of *Protopterus*. ×4.

9. The left pectoral fin of *Cestracion philippi*. Young ♀, dorsal aspect. Half nat. size.

10. The basal portion of a similar fin; same aspect. Adult. (After Huxley.) Reduced to the same scale as fig. 9 for sake of comparison.

11. The left pectoral fin of a young *Polypterus*. Ventral aspect. ×2.

12. The left pelvic fin of a young *Chimæra* (*C. monstrosa*), ♂. Ventral aspect. ×1½.

In figs. 5 and 7 the parameres not represented in full were all rod-like and unbranched.

The dotted lines in figs. 9 and 12 represent lines of fusion observed; those in figs. 5, 6, and 10 are inferred.

*Reference Letters.*

*cp.* Base of clasper. *f.* Inter-articular ligament. *m.p.* Proximal mesomere. *ms.* Mesopterygium. *mt.* Metapterygium. *pl.* Pelvic girdle. *pr.* Preaxial fin-border. *ps.* Postaxial fin-border. *pt.* Propterygium. *r.* Metapterygial rays.